NATURAL HISTORY, ACTIVITY PATTERNS, AND RELOCATION RATES OF A BURROWING WOLF SPIDER: *GEOLYCOSA XERA ARCHBOLDI* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Wolf spiders in the genus *Geolycosa* are obligate burrowers and sit-and-wait predators which typically retain their first burrow throughout life. In the present study I document the activity patterns, burrow closure, and relocation rates of an exception to this pattern: *G. xera archboldi* McCrone, endemic to the scrub of central Florida. In census studies of five field plots I document mean relocation rates of up to 3.2% per day. The smaller size/age classes made up the majority of the relocating spiders. I found that individual spiders had their burrows closed on 26 ± 7% of census days. These burrow closures lasted an average of 6.8 ± 0.3 days, with 10% of burrow closures lasting longer than 14 days.

Geolycosa wolf spiders are sessile members of a largely vagrant family. In spite of having evolved the burrowing habit and restricting all activity to the vicinity of the burrow mouth they have retained behavioral features associated with their vagrant ancestors. These traits include vagility and the attachment of the egg sac to the spinnerets. Published accounts of *Geolycosa* indicate that these spiders generally remain with one burrow throughout their lives and relocate seldom (Wallace 1942; McQueen 1983; Conley 1985) or never (McCrone 1963; Miller 1989; Richardson 1990). The only exception to this has been reported by Richardson (1990) for a population of *G. wrightii* in the lakeshore dunes of Michigan which relocates more than once every two weeks.

Studies of *Geolycosa* ecology have assumed that relocation is a rare enough event that burrow abandonment can be equated with mortality (McQueen 1983; Conley 1985). However, there have been no studies explicitly testing this assumption. The purpose of this study is to document the rates of relocation and activity of an apparent exception to the rule of extreme site tenacity in the genus *Geolycosa*. I have also quantified burrow closure across the population. In addition, I will present data on the natural history of a species of special concern in Florida, a state undergoing vertiginous rates of development (Edwards 1994).

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NATURAL HISTORY OF THE MODEL SYSTEM

Study area.—The research presented here was performed at Archbold Biological Station, a private research facility 10 km south of Lake Placid in Highlands County, Florida. The communities represented at Archbold are unique to the southern Lake Wales ridge and belong to a class of habitats referred to collectively as 'scrub' (Abrahamson et al. 1984). In the scrub *G. xera* is limited to areas of open sand. This includes unpaved roads, the open sand of rosemary balds, and patches of open sand in the oak scrub. The naturally occurring areas are created by fire (which consumes the leaf litter) and wind (which moves the accumulated leaf fall). In these patches of open sand *G. xera* may be found in densities higher than any recorded for other *Geolycosa* species (Table 1).

Study organism.—*Geolycosa xera xera* McCrone and *G. x. archboldi* McCrone are endemic to the scrub and sandhill communities of the dry uplands of Highlands, Polk, Lake, Orange, and southern Volusia counties in central Florida (McCrone 1963). The subspecies in the present study, *G. x. archboldi*, is restricted to Highlands County.

Geolycosa xera archboldi digs a distinctive vertical burrow 16.6 cm deep (± 3.2 cm standard deviation, $n = 25$). Because little silk is used in their construction, these burrows need to be actively maintained in order to persist. A brief rainfall is sufficient to wash burrow mouths closed.

Table 1.—Summary of *Geolycosa* population density estimates for adult females. Adult females are used as this is more widely reported than total population density. Number of samples indicates the number of independent areas or populations studied (modified from Richardson 1990, p. 44).

Species	Spiders/m²	Number of samples	Locale	Source
G. domifex	0.03	1	Ontario	McQueen 1978
G. rafaelana	0.11 ± 0.07	5	New Mexico	Conley 1984
G. wrightii	0.07	1	Michigan	Richardson 1990
G. missouriensis	0.01 ± 0.02	14	Oklahoma	Richardson 1990
G. xera archboldi	0.49 ± 0.25	8	Florida	This study

I saw spiders reopen burrows within minutes of closure due to rainfall or my inadvertently stepping on the burrow mouth. I found that burrow diameter is closely correlated with body size ($P < 0.0001$, $r = 0.92$, $n = 161$) as has been recorded for other *Geolycosa* species (McQueen 1983; Miller & Miller 1984). The foregoing discussion shows how detailed information on the size structure, distribution, and abundance of *G. xera* may be gathered on the basis of burrow characteristics alone.

Geolycosa xera is active year-round. I observed adult females in all seasons, mature males in the fall through spring (see also McCrone 1963) and hatchlings in March through July. Clutch sizes are small (mean ± standard deviation: 24.0 ± 9.0, $n = 5$) compared to an average of 203 for *G. domifex* (McQueen 1978) and 179 for *G. missouriensis* (Richardson 1990). I saw in two successive years (1992, 1993) that the first annual hatchling dispersal from the maternal burrow occurred in mid-to-late March. Hatches were observed throughout the following spring and summer months, but never with the synchrony of the first hatch of the year. I saw no obvious climatological correlates of the dispersal event to explain this synchrony. March is during the dry season in Florida, and the weather is fairly constant. The long breeding season, coupled with year-round activity, the size-class distributions noted above, and observations of captives I have held in the lab for extended periods lead me to believe that *G. xera* matures in 18–24 months. This is similar to published accounts for other *Geolycosa* species (Wallace 1942; McCrone 1963; McQueen 1978; Miller & Miller 1987).

METHODS

Activity and relocation rates.—I established five 2.0 × 2.0 m unenclosed census plots in patches of open sand in scrubby flatwoods. These census plots were all at least several meters apart in distinct and separate sand patches. I censused these plots every other day from 6 March until 3 May 1991. Using dial vernier calipers, at each census I measured the burrow mouth diameter of new burrows to the nearest 0.1 mm and marked them with a numbered surveyor's flag. I also noted whether previously flagged burrows were open or closed. I estimated the mean length of burrow closure periods from those burrow closures which were initiated and terminated within the census period. Extended burrow closure was assumed to be initiated and terminated by the spider. I calculated the percent of censuses in which the individual burrows were closed by dividing the number of censuses the burrow was closed by the total number of censuses for those individual burrows which were both active at the end of the census period and censused at least 10 times. As these data were taken from five defined census plots I report the means and standard deviations as calculated from census plot means.

For the estimates of relocation rates I only considered those burrows found open after the first 14 days of the census period (this minimized the counting of reopened burrows as new, see results below). I also did not count hatchlings in order to avoid inflating relocation rates by including recruitment.

Characterization of relocating individuals.—I enclosed a naturally-occurring habitat patch approximately 12.5 m² with sheet metal flashing. This site was chosen for the study of size-classes and movement as it had a larger population of *G. xera* (approximately 100 individuals) than the census patches used above. In order to examine the relative sizes of relocating *versus* resident individuals, I arbitrarily divided the total number of new burrows for the period (10–18 July 1990) into four size classes and compared these data
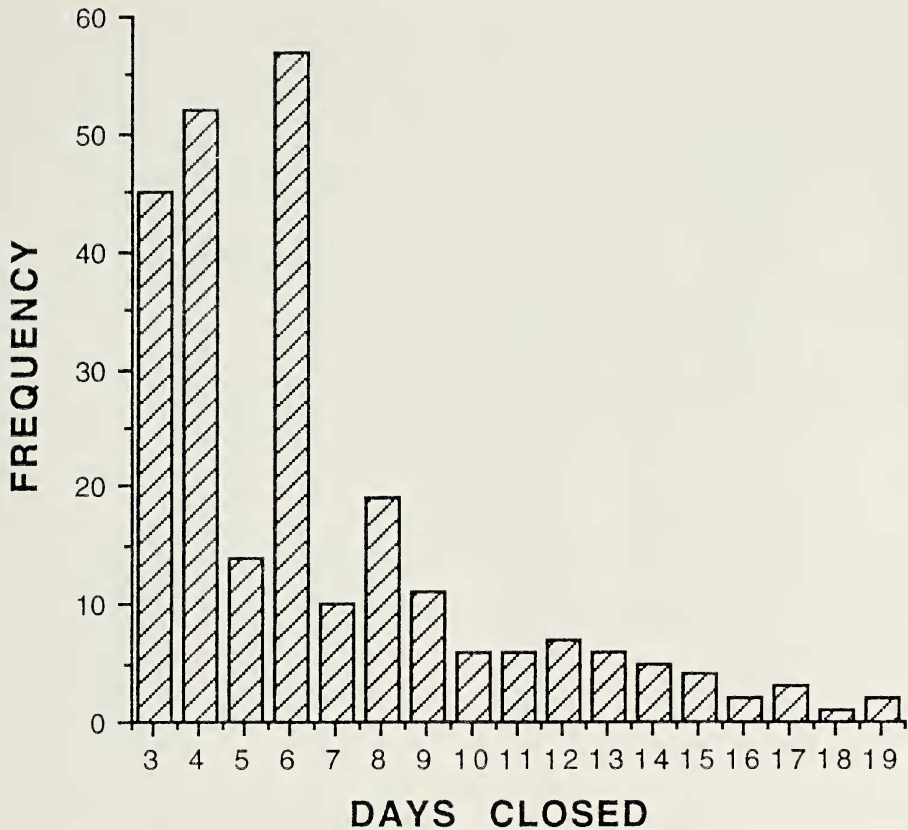
Figure 1.—Duration of burrow closures for a population of marked *Geolycosa xera archboldi* burrows censused every other day in five 4.0 m² open census plots at Archbold Biological Station, Highlands County, Florida (*n* = 250 burrow closures).

to the four size classes of the long-term residents active on 14 July.

RESULTS

Activity and relocation rates.—I found that 90% of burrow closures lasted 14 days or less (Fig. 1). The duration of burrow closures was 6.8 ± 0.3 days (mean ± SD, *n* = 5). Individually, spider burrows were closed 26.0 ± 7.0% (*n* = 5) of

census days. The proportion of new burrows found at each census was 2.0 ± 0.9% per day (*n* = 5, Table 2). This represents my estimate of the relocation rate.

Characterization of relocating individuals.— New burrows belonged predominately to the smaller size classes (Fig. 2). Larger, and thus older, spiders are less likely to change burrow sites than the smaller, younger individuals.

DISCUSSION

Geolycosa xera exhibits unexpectedly high relocation rates for a fossorial spider. Whether the rates I measured in the spring remain as high throughout the year is unknown. However, these results indicate that *Geolycosa* wolf spiders may not all be as sedentary as previously thought.

Given the energetic cost implicit in burrow construction and the risk of predation involved in leaving the security of a burrow, it would be predicted that these spiders would only move in extreme circumstances. Dispersal is assumed to

Table 2.—Summary of relocation rates of *Geolycosa xera archboldi* at Archbold Biological Station in five 4.0 m² census plots, 22 March to 19 April 1991.

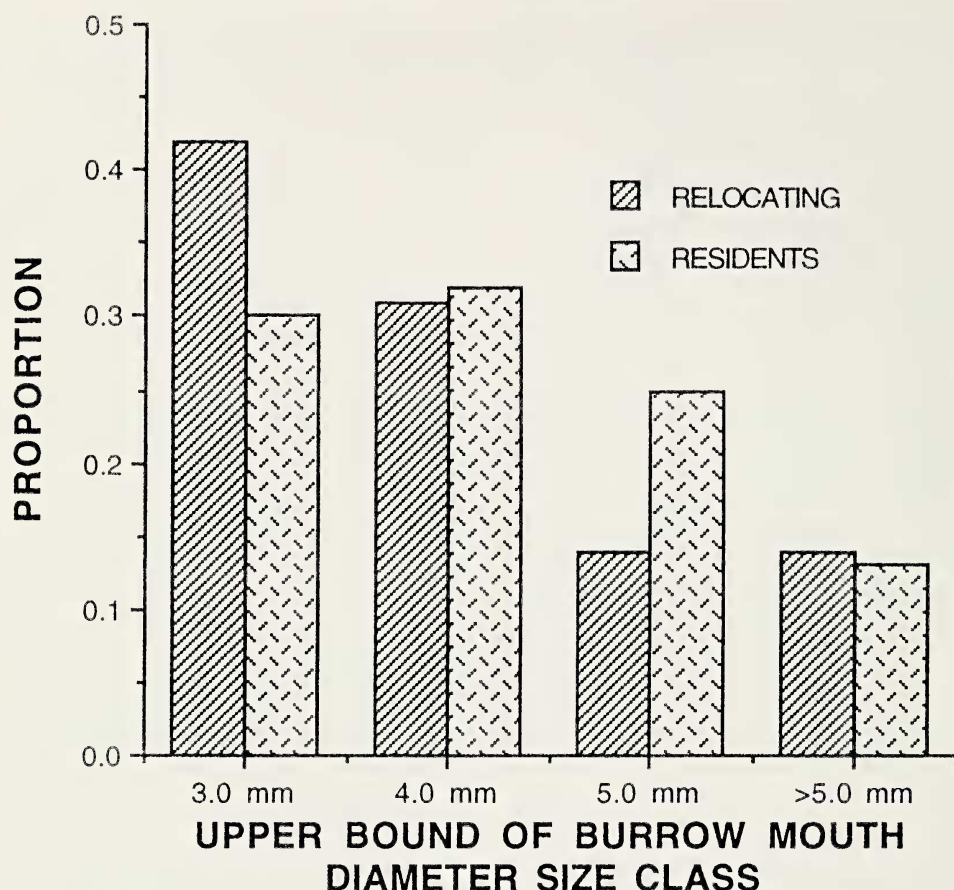| Site	Density (spiders/m²)	Mean daily relocation rate (%)
1	7.20	1.0
2	4.75	1.4
3	2.54	3.2
4	2.04	1.8
5	1.41	2.5

Figure 2.—Composition of a population of *Geolycosa xera archboldi* at Archbold Biological Station. 'Relocating' (*n* = 36) are from new burrows found at daily censuses 10–18 July 1990. 'Residents' (*n* = 73) denotes burrows open on 14 July 1990 (exclusive of 'Relocating').

be risky; and therefore, many studies of dispersal and migration have looked for an adaptive explanation for animal movement (Southwood 1962; Gaines & McClenaghan 1980; Johnson & Gaines 1990). There are no data on the cost of burrow construction in *Geolycosa*; however, there are data which can give us an indication. Culik & McQueen (1985) studied activity patterns and metabolic rates in *G. domifex* and found that movement on the surface elevated metabolic rates 220%, and moving up and down the burrow elevated rates 1780%. As burrow construction involves moving sand up the burrow to the surface, burrow construction should be even more costly than moving up and down the burrow unburdened. Janetos (1987) has documented that there is an inverse correlation between relocation rates and web cost in web spiders. While the evolutionary scenario for web-spiders may not extend to burrow-building spiders, a burrow is likely to represent a long-term investment in a site.

The higher rates of relocation for the younger spiders I found are consistent with patterns reported by other workers (Conley 1985). Why younger spiders are more likely to relocate than older individuals is unknown. I do not feel that relocation to find a better microhabitat site is responsible given that all size/age classes of *G. xera* may be found in close proximity to each other. It may be that stochastic events (e. g., burrow collapse) or territorial interactions with neighbors may be responsible.

I have no data on foraging and relocation rates for *G. xera*, but have observed several possible stochastic mechanisms to explain burrow abandonment. I have seen excavations at the burrow mouth which I attributed to predation attempts which may have been the cause of subsequent

burrow abandonment due to damage to the fragile burrow. I have twice observed that ants invading the burrow to pirate prey elicit a spectacular and immediate response: the spider bolts from the burrow and jumps up into the nearest vegetation. I have three times observed attacks by neighboring conspecific burrow holders on smaller individuals engaging in burrow maintenance behaviors. I have also seen burrow abandonment correlated with encroaching leaf litter.

The burrow of *Geolycosa* wolf spiders may represent both a prison and refuge. Given the cost of construction and maintenance, these spiders may have evolved a foraging strategy and life history centered on the burrow more like those other obligate fossorial spiders, the mygalomorphs, and very unlike their peripatetic confamilials. It seems probable that the obligate fossorial habit of *Geolycosa* evolved in abiotically stringent habitats such as sand dunes. However, *Geolycosa* can make up for this restriction to relatively barren and prey-depauperate sandy habitats by foraging for a longer period each day (vagrant lycosids in the scrub are nocturnal). The burrow permits individuals to shuttle between the thermally extreme conditions at the surface while foraging and the more moderate thermal environment of the burrow. The evolution of the fossorial habit also allowed an eresid to invade barren sand dunes in the Namib desert (Lubin & Henschel 1990).

Geolycosa xera archboldi has the most restricted range of any known *Geolycosa* wolf spider. It lives in a specific microhabitat within an endangered ecosystem (Edwards 1994; Marshall 1994). While the densities it achieves at suitable sites can be quite high, unless the habitat is periodically burned, populations decline as patches of open sand are covered with leaf litter. *Geolycosa x. archboldi* cannot tolerate any leaf litter covering the burrow mouth, and will abandon any burrow covered with leaf fall. *Geolycosa xera* is an excellent indicator species of the quality and health of patches of scrub in Florida's beleaguered uplands habitats: it is active year-round, sensitive to burn frequency, and identifiable on the basis of burrow characteristics and locale alone. Populations persist at far smaller patches of scrub than do endemic vertebrates (e. g., Florida scrub jays).

ACKNOWLEDGMENTS

LITERATURE CITED

Abrahamson, W. G., A. F. Johnson, J. N. Layne, & P. A. Peroni. 1984. Vegetation of the Archbold Biological Station: an example of the southern Lake Wales Ridge. Florida Scient., 47:209–250.

Conley, M. R. 1984. Population regulation and prey community impact of *Geolycosa rafaelana* (Chamberlin) (Araneae: Lycosidae). Dissertation, New Mexico State Univ., Las Cruces, New Mexico.

Conley, M. R. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). Oecologia, 67:71–75.

Culik, B. M. & D. J. McQueen. 1985. Monitoring respiration and activity of the spider *Geolycosa domifex* (Hancock) using time-lapse television and CO_2 gas analysis. Canadian J. Zool. 63:843–846.

Edwards, G. B. 1994. McCrone's burrowing wolf spider. Pp. 232–233, *In*: Rare and Endangered Biota of Florida, Vol. IV., Invertebrates (M. Deyrup & R. Franz, eds.). Univ. Florida Press, Gainesville, Florida.

Gaines, M. S. & L. R. McClenaghan, Jr. 1980. Dispersal in small mammals. Ann. Rev. Ecol. Syst., 11:163–196.

Janetos, A. C. 1987. Web-site selection: are we asking the right questions? Pp 9–22, *In*: Spiders: Webs, behavior, and evolution. (W. A. Shear, ed.). Stanford Univ. Press, Stanford, California.

Johnson, M. L. & M. S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Ann. Rev. Ecol. Syst., 21:449–480.

Lubin, Y. & J. Henschel. 1990. Foraging at the thermal limit: burrowing spiders (*Seothyra*, Eresidae) in the Namib desert dunes. Oecologia, 84:461–467.

Marshall, S. D. 1994. Territorial aggregation in the burrowing wolf spider *Geolycosa xera archboldi* McCrone: Formation, maintenance, and consequences. Dissertation, Univ. Tennessee, Knoxville.

McCrone, J. D. 1963. Taxonomic status and evolutionary history of the *Geolycosa pikei* complex in

the South-eastern United States (Araneae, Lycosidae). American Mid. Nat., 70:47–73.

McQueen, D. J. 1978. Field studies of growth, reproduction, and mortality in the burrowing wolf spider *Geolycosa domifex* (Hancock). Canadian J. Zool. 56:2037–2049.

McQueen, D. J. 1983. Mortality patterns for a population of burrowing wolf spiders, *Geolycosa domifex* (Hancock), living in southern Ontario. Canadian J. Zool., 61:1263–1271.

Miller, G. L. 1989. Subsocial organization and behavior in broods of the obligate burrowing wolf spider *Geolycosa turricola* (Treat). Canadian J. Zool., 67:819–824.

Miller, G. L. & P. R. Miller. 1984. Correlations of burrow characteristics and body size in burrowing wolf spiders (Araneae: Lycosidae). Florida Ent., 67: 314–317.

Miller, G. L. & P. R. Miller. 1987. Life cycle and courtship behavior of the burrowing wolf spider *Geolycosa turricola* (Treat) (Araneae, Lycosidae). J. Arachnol., 15:385–394.

Richardson, R. K. 1990. Life history, soil associations, and contests for burrows in a burrowing wolf spider, *Geolycosa missouriensis* Banks. Dissertation, Univ. Oklahoma, Norman, Oklahoma.

Southwood, T. R. E. 1962. Migration of terrestrial arthropods in relation to habitat. Biol. Rev., 37: 171–214.

Wallace, H. K. 1942. A revision of the burrowing spiders of the genus *Geolycosa* (Araneae, Lycosidae). American Mid. Nat., 27:1–62.